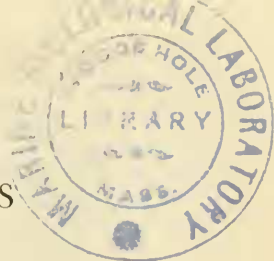


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THE CYTOGENETICS OF HYBRIDS IN BROMUS II.  
BROMUS CARINATUS AND BROMUS ARIZONICUS

BY

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INTRODUCTION

THE FACT that *Bromus carinatus* H. and A. and its relatives constitute a complex of polyploid entities, mostly if not entirely of allopolyploid or hybrid origin, has been brought out in the first paper of this series (Stebbins and Tobgy, 1944). In an earlier survey of chromosome numbers (Stebbins and Love, 1941) the octoploid number of chromosomes ( $2n=56$ ) was counted in all representatives of this complex collected in California. Counts made by us of collections from Oregon, Washington, Idaho and British Columbia have revealed the same number, so that we can state with some assurance that the Pacific Coast members of this complex are predominantly if not entirely octoploid, with the exception of a type originally collected by one of us (Harlan) in Central Arizona. The 28 collections of the *B. carinatus* complex made in this state were found to be divided into two series on the basis of morphological and ecological characteristics. The first series, found mostly in desert washes, roadsides, and waste places at lower altitudes consists of strictly annual plants with relatively long awns; while the second, found predominantly at altitudes of 5000 feet (1500 meters) or higher, consists of perennials, with broad glumes; usually many-flowered spikelets, and shorter awns. The first series agree with the original description of *B. carinatus* var. *arizonicus* Shear (1900), and would be identified as *B. carinatus* according to

the key of Swallen (1942) in the Arizona flora of Kearney and Peebles. The second, since all but one of the specimens collected have essentially glabrous foliage, would be considered *B. polyanthus* Shear, according to the treatment of Swallen (*loc. cit.*). Chromosome counts on five different collections of this second series revealed 56 chromosomes in them, as in Pacific Coast members of the complex. A detailed description of one collection of it (no. 116), with an account of its crossing relationships with other octoploid species, is presented elsewhere (Stebbins and Tobgy, 1944).

The annual, long-awned series, on the other hand, was found to possess uniformly the somatic number  $2n=84$ , or 42 bivalents at meiosis, in material from 21 different collections (see map, fig. 4). Furthermore, the same chromosome number was found in a similar annual form from Tehachapi, Kern County, California. When these duodecaploids were grown in the same field at Berkeley along with a large series of octoploids from California as well as Arizona, it was found that certain morphological characteristics made them readily distinguishable from the perennial or subperennial, long-awned octoploid types from lower altitudes in California, as well as from the short-awned octoploids found at higher altitudes in both states. For this reason, the specific distinctness of the 84-chromosome type was suspected, and the testing of this hypothesis by means of hybridization seemed desirable. The results of this hybridization and their implications in regard to the status and possible origin of the 84-chromosome type are here presented.

#### MATERIAL AND METHODS

Seeds from the Arizona collections were all planted in the field in the summer of 1941. Although each progeny from a single collection was with a few exceptions remarkably uniform, there was a great deal of variation between collections (Harlan, in press). Some of the seedlings behaved like desert ephemerals, producing only one or two tillers, which flowered in a few weeks when only 10 or 15 cm high, and produced only 2 or 3 spikelets, dying when the seed matured. Others behaved like winter annuals, and in the spring produced very tall plants with several tillers and large panicles. It was from one of the latter type that the parent stock for hybridization with octoploid *B. carinatus* was selected. The particular collection, no. 125, came from south of Lake Meade, near Boulder Dam, Mojave County. The octoploid strain used for hybridization was a typical *B. carinatus* strain from Berkeley, represented in the University of California Herbarium by the collection Stebbins no. 2677, and described elsewhere as strain no. 5 (Harlan, in press; Stebbins and Tobgy, 1944). The hybridization was made in the field in May 1942, by Mr. Henry Moser, according to the method described earlier (Stebbins and Tobgy, *loc. cit.*). The cytological techniques used are described in the same paper.

MORPHOLOGY AND SYSTEMATIC DESCRIPTION OF  
THE SPECIES AND THE HYBRID

The morphological and cytological data presented below leaves no doubt that the 84-chromosome type is a species sharply distinct from any now recognized in the *B. carinatus* complex, even though its diagnostic characteristics are somewhat meager. Therefore, a taxonomic description of it will be given at the outset, so that it may thereafter be referred to by its correct name. Although the type specimen of Shear's *B. carinatus* var. *arizonicus* has not been seen, and the original description is somewhat scanty, nevertheless there is little doubt that it belongs to the 84-chromosome species described here. All of the collections made by Harlan from situations similar to Tucson, its type locality, are of this species, and it is the only member of the complex known from lower altitudes in Arizona. One collection, no. 105, in which 84 chromosomes were counted, came from the Santa Cruz Valley only 35 miles from the type locality. It may be described as follows (the taxonomic section is the work of the senior author).

***Bromus arizonicus*** (Shear) Stebbins n. comb.

Planta annua; culmi humiles vel alti; paniculae parvae spiculis paucis, vel ampla spiculis numerosis; glumae elongatae, secunda infinam lemmam aequans; lemmata ad marginem hirsuta, dorso scabra vel glabra, lemmata superiores conspicue bidentata.

Plants annual; culms 15–140 cm high, with 3–5 nodes. Leaves somewhat glaucous, glabrous or pubescent. Panicle sometimes much reduced, but in well developed plants ample, the branches spreading, in groups of 5–6 at the lower nodes, the longest bearing 5–8 spikelets; branches often finely hirsute, the hairs more slender than in *B. carinatus*. Spikelets mostly 5–7 flowered; glumes subequal or distinctly unequal, *elongate, the upper glume about equalling in length the lowest lemma*. Lemmas of medium length, mostly 11–14 mm long, *sparsely or densely hirsute near the edges, short-scabrous on the back, bidentate, the teeth rather prominent, those of the upper lemmas often with the lateral nerves extending into them*.

*Bromus carinatus* var. *arizonicus* Shear, U. S. Div. Agrost, Bull. no. 23: 62.1900. Type in the U. S. National Herbarium, from near Tucson, Arizona, C. G. Pringle in 1884. *B. carinatus californicus* Shear, U. S. Dept. Agr. Div. Agrost. Bull. 23:60, at least in part.

Central and southern Arizona to southern and central California, in desert areas and open, disturbed ground of valleys; an introduced weed in the north-western portion of its present range. The following specimens, in the herbaria of the University of California (UC) and the California Academy of Sciences (CAS), are typical: CALIFORNIA: Mark West Creek, *Bolander* 3985 (UC); Davis, Yolo County, *Stebbins* 3356 (UC); Alcalde, Fresno County, *Eastwood* 13492 (CAS); Tulare, *Davy* 3055 (CAS); Kettleman City, Kings County,

Hoover 442 (UC) ; Bakersfield, Kern County, *Davy* 1896 (UC) ; San Emigdio Cañon, Kern County, *Davy* 1985 (UC) ; Tehachapi, Kern County, *Harlan* 128 (UC) ; Paso Robles, San Luis Obispo County, *Barber* in 1900 (UC) ; Santa Maria, Santa Barbara County, *Eastwood* 344 (CAS) ; Pasadena, Los Angeles County, *Grant* 117, 117a (UC, CAS) ; Claremont, Los Angeles County, *Davy* in 1902 (UC) ; San Bernardino, *Parish* in 1889 (UC) ; Colorado Desert, Riverside County, *Hall* 5980 (CAS) ; Fall Brook, San Diego County, *Jones* 3108

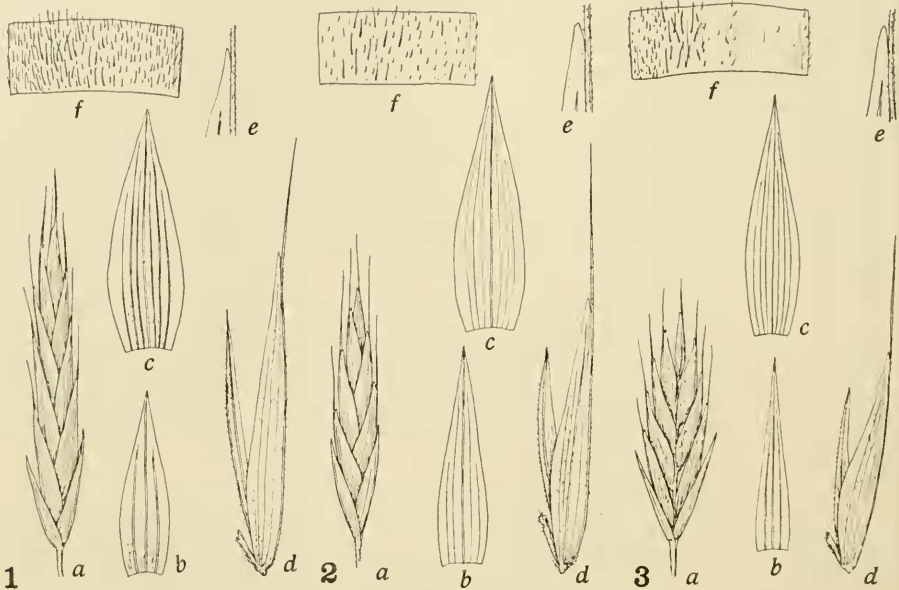


Fig. 1. *Bromus carinatus*, strain no. 5.

Fig. 2. *Bromus arizonicus* × *carinatus*, no. 306.5.

Fig. 3. *Bromus arizonicus*, no. 311.1 (progeny of Harlan no. 125). Figs. 1a, 2a, 3a, spikelets, × 1. Figs. 1b, 2b, 3b, lower glumes; 1c, 2c, 3c, upper glumes; 1d, 2d, 3d, lemmas and paleae, all × 2. Figs. 1e, 2e, 3e, apices of lemmas, × 4. Figs. 1f, 2f, 3f, portions of surface of lemmas, with midrib at right and margin at left, showing pubescence, × 8.

(CAS) ; San Diego, *Orcutt* 1178 (UC) ; between Del Mar and Lower California, *Lemmon* in 1888 (CAS) ; Santa Catalina Id., *Brandegge* in 1890 (UC) ; Santa Cruz Id., *Brandegge* in 1888 (UC) ; Santa Rosa Id., *Hoffmann* in 1929 (CAS) ; San Clemente Id., *Murbarger* 56 (UC) ; San Nicolas Id., *J. T. Howell* 8226 (CAS). BAJA CALIFORNIA : San Quintin, *Epling and Stewart* in 1936 (CAS) ; 24.3 miles east of Rosario, *Wiggins* 5291 (UC, CAS). ARIZONA : Wickenburg, Maricopa County, *W. W. Jones* in 1921 (UC) ; Tempe, Maricopa County, *Gillespie* 5519 (UC) ; Fort Lowell, *Thorner* 535 (UC) ; 25 miles southeast of Lake Meade, Mohave County, *Harlan* 125 (UC) ; east of Kingman, Mohave County, *Harlan* 123 (UC) ; Pinal Mts., southwest of Globe, Gila County, *Harlan* 112 (UC) ; Salt River Canyon, Gila County, *Harlan* 115 (UC) ; Sacaton, Pinal County, *Harlan* 103 (UC) ; east of Flor-

ence, Pinal County, *Harlan* 107 (UC); Red Rock, Pinal County, *Harlan* 105 (UC).

As stated previously, the chromosome number  $2n=84$  has been determined in all of the Harlan collections cited.

Without having seen the type specimen, the writer cannot determine whether *B. arizonicus* is the same as *B. carinatus californicus* Shear, or *B.*



Fig. 4. Map showing distribution of Harlan collections of *Bromus arizonicus* ( $2n = 84$ ), solid circles, and *B. polyanthus* vel aff. ( $2n = 56$ ), hollow squares, in Arizona. The 5000 foot contour level is drawn.

*californicus* Nutt. Nuttall's specific name is a *nomen nudum* (cf. Shear 1900), and his specimen, according to Shear, "is a mere scrap," of which the locality of collection is indefinite. Nevertheless, the specimens cited by Shear under *B. carinatus californicus*, since all come from San Diego or Lower California, are very likely *B. arizonicus*.

The characteristics which distinguish *B. arizonicus* from all other members of the subgenus *Ceratochloa* in the Western United States are the *strictly* annual habit (the plants always die when the seeds have matured), the elongate glumes, the hirsute pubescence near the margin of the lemmas, and the rather prominent lobes of at least the upper lemmas (fig. 2). All of the typical, octoploid members of the *B. carinatus* complex as grown in Berkeley produced some new tillers after the seed had ripened, except when the plants



were obviously diseased. In all of them the lowest lemma is distinctly longer than the upper glume; its pubescence, whether long or short is more or less evenly distributed over the surface; and the lobes are very short, with the lateral nerves ending far below their base (fig. 1).

The relative distributions of *B. arizonicus* and the octoploids referred to *B. polyanthus* are shown on a map (fig. 4) giving the localities from which chromosome counts were obtained. Only one collection from California has

TABLE 1  
COMPARISONS OF THE DIAGNOSTIC CHARACTERISTICS OF *B. carinatus*,  
*B. arizonicus*, AND THEIR F<sub>1</sub> HYBRID

	<i>B. carinatus</i> (no. 5)	F <sub>1</sub> hybrid (no. 125 × no. 5)	<i>B. arizonicus</i> (no. 125)
Number of nodes of culms . . . . .	5-6	5	4-5
Pubescence of top node . . . . .	+ below	++ throughout	+ throughout
Pubescence of upper culm leaf . . . . .	+ lower	++ upper + lower	+ upper 0 lower
Maximum number of branches at node of panicle . . . . .	5-8	4-5	4-6
Maximum number of florets per spikelet . . . . .	8-9	7-9	6-7
Length second glume . . . . .	14.3	16.0	12.4
Length second lemma . . . . .	16.4	15.2	12.3
Ratio, glume/lemma . . . . .	0.87	1.05	1.01
Pubescence of second lemma . . . . .	++ throughout	++ margins + back	++ margins 0-+ back
Lobes of upper lemmas . . . . .	small	intermediate	prominent

been counted, that from Tehachapi (no. 128), but the external morphology of the other California specimens cited leaves no doubt as to their specific identity. At Davis, California, the northern limit of its known range, *B. arizonicus* is obviously a recent introduction along the railroad tracks, and it is very likely introduced at the San Joaquin Valley localities also.

The particular strain of *B. arizonicus* used for hybridization was one of the most vigorous and latest in flowering of all. As recorded elsewhere (Harlan, 1942; Stebbins and Tobgy, 1944), the no. 5 strain of *B. carinatus* is also a very vigorous one. It is about intermediate or somewhat late in flowering compared to other Berkeley strains, but earlier than most of the montane types. It is distinguished from most other *B. carinatus* strains from Berkeley by its rather large spikelets and lemmas; the average length of the lemmas and awns in *B. carinatus* as a whole is not very different from that in *B. arizonicus*. The chief distinguishing characteristics of the two parental strains are given in Table 1.

No hybrid seeds were obtained out of 42 florets emasculated when *B. arizonicus* was used as the pollen parent on *B. carinatus*. In the reciprocal cross,

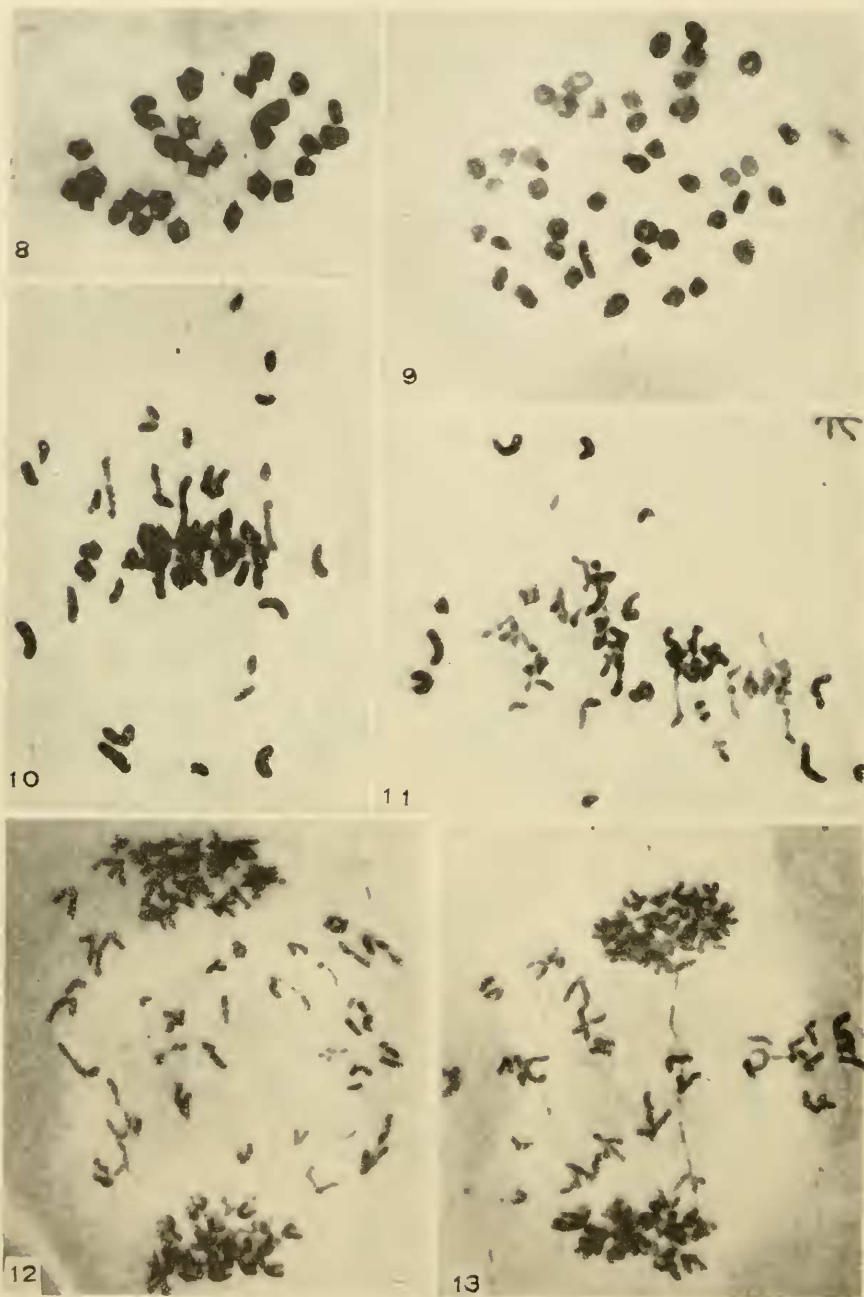
*B. arizonicus* ♀ × *B. carinatus* ♂, 37 seeds were obtained out of 40 florets emasculated. Of these, 10 were sown in September, 1942. Four were lost through an accident, and six were planted in the field in November. Of these 4 turned out to be hybrids. Morphologically, they were intermediate between their parents, except that in number of florets per spikelet they were nearer their *B. carinatus* parent, and in relative size of glumes and lemmas, like *B. arizonicus* (Table 1). They proved to be completely pollen and seed sterile, a condition which would be expected from the cytological situation described below. Three of them died during May, 1943, even before their annual *B. arizonicus* parent. A fourth showed some tendency to grow out after being cut back, as does *B. carinatus*, but died during the fall of 1943.

#### CYTOLOGY OF THE PARENTS AND HYBRID

1. *B. carinatus*: The meiotic chromosome behavior of strain no. 5 of *B. carinatus* used in this study has been reported earlier (Stebbins and Tobgy, 1944). The main features may be outlined here. At diakinesis and I-meta-



Figs. 5-7, chromosome pairing at first metaphase in: 5, *B. carinatus*; 6, *B. arizonicus*; 7, *B. arizonicus* × *carinatus*. All reproduced × 1300.



Figs. 8-13. Photomicrographs showing chromosome behavior, all reproduced  $\times 800$ . 8, *B. carinatus*, I metaphase; 9, *B. arizonicus*, diakinesis; 10 and 11, *B. arizonicus*  $\times$  *carinatus*, I metaphase; 12 and 13, *B. arizonicus*  $\times$  *carinatus*, I anaphase.



phase there were always 28 bivalents; no univalents or multivalents were ever seen. Seven bivalents could be distinguished by their conspicuously large size, while the remaining 21 bivalents were uniformly smaller and may therefore be termed medium-sized (figs. 5 and 8). At I-metaphase most of the bivalents had two chiasmata, one in each arm, and occasionally some of the large bivalents had three chiasmata. The majority of the bivalents, large and medium-sized, were therefore pairing in both arms, although rarely one or two of them were pairing in one arm only. In 9 per cent of the I-anaphase cells and in 1 per

TABLE 2  
CHROMOSOME PAIRING AT MEIOSIS IN *Bromus arizonicus* × *carinatus*

Combination				No. of cells*	Per cent
$m_{III}$	$m_{II}$	$m_I$	$l_I$		
7	14	14	7	12 (2)	33.5
6	15	15	7	6	16.2
5	16	16	7	6	16.2
4	17	17	7	9 (2)	24.3
3	18	18	7	2 (1)	5.4
2	19	19	7	2 (1)	5.4
Total.....				37	100.0

\* The numbers in parentheses refer to 6 cells in which two of the chromosomes regularly forming a  $m_{II}$  appeared instead as  $2m_I$ .

cent of the II-anaphase cells one inversion bridge and a fragment were seen. Almost 99 per cent of the tetrads had 4 normal microspores; in the remaining 1 per cent, one or two micronuclei were also present. There was 81.0 per cent stained pollen.

2. *B. arizonicus*: At diakinesis and I-metaphase of *B. arizonicus* there were always 42 medium-sized bivalents (figs. 6 and 9); univalents and multivalents were significantly missing. There was no differentiation into large and small bivalents and none of the bivalents could be classified in the large size category characteristic of seven bivalents in *B. carinatus*. In almost half of the I-metaphase cells all the bivalents were paired in both arms and in the other half one, two, or three bivalents were paired in one arm only. There was less inversion hybridity exhibited in the *B. arizonicus* plant examined than in that of *B. carinatus*. Only 1 per cent of the I-anaphase cells and 0.4 per cent of the II-anaphase cells showed one chromatid bridge and one fragment. About 2.5 per cent of the tetrads had one or two micronuclei in addition to the 4 normal microspores, but the remaining 97.5 per cent had 4 large microspores only. There was 90 per cent stained pollen.

3. *B. arizonicus* × *B. carinatus*. The  $F_1$  hybrid plants ( $2n=70$ ) between *B. arizonicus* ( $2n=84$ ) and *B. carinatus* ( $2n=56$ ) received 42 medium-sized

chromosomes from *B. arizonicus* and 21 medium + 7 large chromosomes from *B. carinatus*. Thirty-seven cells at I-metaphase were completely analyzed in the hybrid (Table 2).

Pairing of the parental chromosomes followed a comparatively simple scheme which may be described as follows:

1. The 7 large chromosomes from *B. carinatus* were always seen as 7 unpaired univalents ( $m_I$  in the table).
2. At least 2 sets of 7 medium chromosomes from *B. arizonicus* also appeared as 14 unpaired univalents ( $m_{II}$  in the table).
3. At least 14 medium bivalents were almost always seen ( $m_{III}$  in the table); these being formed from the consistent pairing of 2 sets of 7 medium chromosomes from *B. arizonicus* with 2 corresponding sets from *B. carinatus*.
4. A maximum number of 7 trivalents was formed ( $m_{III}$  in the table); these resulted from partial or complete homology between one set from *B. arizonicus*, another from the same species, and a third from *B. carinatus*. When the maximum number of 7 trivalents was formed, there were 14 medium bivalents, 14 medium univalents and 7 large univalents in the cell. With decreasing numbers of trivalents, the number of bivalents and univalents was correspondingly increased. A typical I-metaphase cell is shown in figure 7, and two other cells in figures 10 and 11. The percentage of cells with these varying numbers of trivalents is given in the last column of Table 2. A slight reduction in the normal pairing in a few cells was found (cf. footnote, Table 2).

TABLE 3  
SPORAD ANALYSIS IN *B. arizonicus* × *carinatus*

Number of cells in sporad	Number of micronuclei			Totals	Per cent
	7-11	12-16	17-21		
4 cells.....	20	51	27	107	58.5
5 cells.....	15	23	6	44	24.0
6 cells.....	8	13	4	25	13.7
7 cells.....	2	4	1	7	3.8
Totals.....	54	91	38	183	....
Percentages.....	29.5	49.7	20.8	..	100.0

There was good evidence of extensive inversion hybridity in the  $F_1$ . This was shown by bridge-fragment configurations in 48.5 per cent of the cells at I-anaphase and by 16.5 per cent of the cells at II-anaphase. Usually only one bridge and occasionally two were seen at I-anaphase, and only once was a cell with three bridges encountered (fig. 13). All the bridges at II-anaphase were genuine second division bridges and not relics from the first division. Therefore the extent of inversion hybridity in the hybrid may be represented as one bridge in 65 per cent of the pollen mother cells. It could not be always determined whether the inversions were confined to the bivalents or were found in the trivalents also, but evidence was obtained of bridges in both types of configurations. Therefore it is likely that the two groups of parental

chromosomes which regularly pair differ by inversions as well as the two partly homologous sets from *B. arizonicus* which enter into the trivalents. Since heterozygosity for inversions was found to a small degree in both parents, it is reasonable to suppose that most of the pairing sets differ by at least a few inversions.

The majority of the univalent chromosomes divided equationally and the two daughter univalents separated to the two poles at I-anaphase, but occasionally some of the univalents, though already divided, would fail to undergo the anaphasic separation and would pass entirely to one pole or the other (figs. 12 and 13). There was excessive chromosome lagging at the second division, which, together with that at the first division, may best be represented by the very complex condition of the sporads (Table 3).

With such conditions prevailing in the sporads the repeated observation of complete sterility of both pollen and ovules is the expected condition.

### DISCUSSION

*Specific distinctness of B. arizonicus.* The experimental evidence presented here shows that, because of the extreme abnormality of meiosis in their  $F_1$  hybrid, and the complete inviability of both pollen and ovules, *B. arizonicus* and *B. carinatus* are completely incapable of interbreeding, that is of exchanging genes. Therefore, they would be recognized as distinct species under any modern definition of this entity (cf. Dobzhansky 1941, p. 373). Furthermore, the cytological evidence indicates that *B. arizonicus* would be equally intersterile with any other octoploid member of the *B. carinatus* complex (cf. Stebbins and Tobgy, 1944). The two species clearly are not made up of the same chromosomal material. Out of the haploid complement of 42 in *B. arizonicus*, 21 chromosomes are nearly or quite homologous to 21 of the haploid set of 28 in *B. carinatus*, 7 are partly homologous with 7 of these 21 *carinatus* chromosomes and 14 are entirely different. The resemblance between *B. arizonicus* and *B. carinatus*, therefore, lies principally in their common possession of 21 pairs of medium-sized (m) chromosomes.

*Cytological constitution and possible origin of B. arizonicus.* In another paper (Stebbins and Tobgy, 1944) it was shown that the 21 medium-sized chromosomes (m) in *B. carinatus* are almost completely homologous with the 21 chromosomes which form the entire haploid complement of the South American species, *B. catharticus* Vahl (*B. unioloides* HBK). In that paper, these sets were designated  $\Lambda$ ABBCC, so that the genome formula of the various octoploid members of the *B. carinatus* complex was written as  $\Lambda$ ABBCCLL, LL representing the sets of 7 large chromosomes. The present evidence shows that *B. arizonicus* possesses the  $\Lambda$ ABBCC set, perhaps somewhat modified, but lacks the 7 pairs of large, or the LL chromosomes. Of its other three sets, one may be designated as  $C_2 C_2$ , because of its similarity to one set of the *catharticus* group, this partially homologous set being arbitrarily designated as the CC one. The remaining two sets of *B. arizonicus* may be designated DDEE.

Thus the genome formula of *B. arizonicus* may be written AABBC<sub>1</sub>C<sub>1</sub>C<sub>2</sub>C<sub>2</sub>DDEE. It should be clearly understood that this formula is used only to express pairing relationships; the actual genic content of the genomes probably varies considerably from species to species, and they undoubtedly differ in the various species by minor structural variations.

This cytological constitution indicates that *B. arizonicus* is an allopolyploid derived by chromosome doubling from a hybrid between *B. catharticus* or a close relative of it and some other species with 21 pairs of medium-sized chromosomes. The identity of this other parent is not yet established, but based on the morphological differences between *B. arizonicus* and *B. carinatus*, its main features can be postulated. They are as follows:

1. It should be an annual, preferably found in desert or at least semiarid situations.
2. Its panicle branches should be slender, but should be glabrous or finely short-pubescent, rather than coarsely scabrous as in *B. catharticus*.
3. Its glumes should be elongate, definitely exceeding the lower lemmas. The outer glume should have chiefly 3 nerves.
4. Its lemmas should be rounded on the back or weakly keeled, should be long-hirsute near the margins, conspicuously bidentate at the apex, and long-awned.
5. It should form a maximum of 7 bivalents in hybrids with *B. catharticus* or *B. carinatus*.

The morphological characteristics listed here are found in only one species of *Bromus* known to us, *B. Trinii* Desv. This species also has the required 21 pairs of medium-sized chromosomes, as determined by Knowles (1944) as well as by the senior author. Its pairing relationships with *B. catharticus* and *B. carinatus* have not yet been tested. The hypothesis may, however, be advanced that *B. arizonicus* is an allopolyploid derived from *B. catharticus* and *B. Trinii* or close relatives of these species. It is hoped that this can be tested in the near future by appropriate hybridization experiments. The hypothesis involves some difficulties from the historical point of view, since both of the putative parents are generally believed to be native only to South America, and to be recent introductions into the area now occupied by *B. arizonicus*. This problem, however, had best be considered after the evidence in favor of the proposed hypothesis has become more definite.

There is one cytological discrepancy found in the pairing behavior of the chromosomes of *B. arizonicus* in the pure species as compared with their behavior in its hybrid with *B. carinatus*. The trivalents found in the hybrid indicates definitely a partial homology between two of the sets in *B. arizonicus*. That they could not possibly consist of two sets from *B. carinatus* and one from *B. arizonicus* is evident from the fact that in another hybrid, *B. carinatus* × *B. mollis*, the chromosomes nearly all remain unpaired, showing that there is little or no homology between any of the four sets found in *B. carinatus* (Knowles 1944). The difficulty is that these two partially homologous sets of *B. arizonicus* should occasionally form quadrivalents in the pure species. However, in several different strains, examined by each of the three authors, the presence of 42 bivalents was observed with strikingly consistent regularity,



and the partial homology between two of the sets was not even suspected until the cytology of the hybrid was studied. Two explanations for this phenomenon are suggested. The first is that advanced by Müntzing and Prakken (1940) for a similar behavior in *Phleum pratense*, which was also found in the same species by Myers (1941). They assume that in *Phleum* and other genera there is a "special genotypically controlled tendency to bivalent formation" (p. 494). The other explanation is that of differential affinity, or preferential pairing, advanced by Darlington (1927, p. 198) to explain the lack of multivalents in the allopolyploid *Primula kewensis*, and by Skirm (1942), to explain the difference in pairing found in two different tetraploids of *Tradescantia*, both obtained from the same diploid hybrid. From the data now at hand, there is no way of concluding which is the best explanation for the situation in *Bromus arizonicus*.

In conclusion, the following points have arisen from this study which are of particular interest to students of the taxonomy of the Gramineae. In the first place, whatever the second parent of *B. arizonicus* is, it most certainly belongs neither to the section *Ceratochloa* nor to the section *Bromopsis*, as postulated for the second parent of the octoploid *B. carinatus* and its relatives (Stebbins and Tobgy, *loc. cit.*). The morphological characteristics listed above would immediately remove the species from the former section, while in the latter the chromosomes are large, like the LL set of *B. carinatus* (Stebbins and Love, 1941). Both *B. carinatus* and *B. arizonicus*, therefore, are allopolyploids from intersectional hybrids, but the two sections thus connected by allopolyploidy are different in each case. Therefore the cytogenetic evidence entirely supports the recognition of *Bromus* as a single genus, rather than the separation of *Ceratochloa* as generically distinct, as has been done by a number of agrostologists. It speaks even more emphatically against the splitting of *Bromus* into several different genera, as was proposed by Nevski (1934).

In the second place, the particular type of relationship which exists between *B. carinatus* and *B. arizonicus* will probably be found to be rather frequent when more genera of this family are studied cytogenetically, since polyploidy is so prevalent in them. They are a typical example of species which are morphologically very similar, and cytogenetically partly very similar and partly very different. Their similarities are due to their common possession of the *B. catharticus* set. Their morphological differences represent, in a much diluted form, the differences between two different sections of the genus. Both of these sections diverge from typical *Ceratochloa* in their much less strongly keeled lemmas and much longer awns; hence both *B. arizonicus* and *B. carinatus* diverge from *B. catharticus* in the same respects. *B. carinatus* and *B. arizonicus* may therefore be spoken of as *allosyngenic amphidiploids* (or allopolyploids), since they differ in respect to one of their original parents, and have the other in common. The likelihood is that in all genera possessing large polyploid complexes, allosyngenic amphidiploids form one of the chief sources of taxonomic difficulty.



## SUMMARY

1. A new species, *B. arizonicus*, is described, based on *B. carinatus* variety *arizonicus* Shear. This species has the somatic chromosome number  $2n = 84$ , as compared with  $2n = 56$  for *B. carinatus*.

2. The hybrid, *B. arizonicus* × *B. carinatus*, can be obtained only when *B. arizonicus* is the female parent. It is morphologically intermediate between its parents and is completely sterile.

3. At meiosis this hybrid regularly shows a maximum of 7 trivalents, with the rest of the chromosomes existing as bivalents and univalents. The 7 large chromosomes obtained from *B. carinatus* have no homologues in *B. arizonicus*, and therefore are always unpaired, as are also 14 medium-sized chromosomes from *B. arizonicus*.

4. The presence of bridge-fragment configurations in either the first or the second division of meiosis in 65 per cent of the pollen mother cells indicates that the chromosomes of two or more of the pairing sets differ by a number of inverted segments.

5. The cytogenetic evidence amply demonstrates the specific distinctness of *B. carinatus* and *B. arizonicus*. Their genomic formulae may be written as follows: for *B. carinatus*  $\Lambda\Lambda B B C_1 C_1 L_1 L_1$ , for *B. arizonicus*  $\Lambda\Lambda B B C_1 C_1 C_2 C_2 D D E E$ . The  $\Lambda$ ,  $B$ , and  $C_1$  sets constitute the chromosomal complements of *B. catharticus*. It is possible that *B. arizonicus* possesses this complement in a slightly modified form.

6. The hypothesis is advanced that *B. arizonicus* is an allopolyploid derived from doubling of the chromosome number in a hybrid between *B. catharticus* or a close relative of that species and some other species with 21 pairs of medium-sized chromosomes, not belonging to the subgenus *Ceratochloa*.

7. The cytogenetic evidence here presented supports the retention of *Bromus*, sens. lat., as a single genus.

8. The relationship of *B. carinatus* and *B. arizonicus* is described as that of allosyngenic amphidiploids. This type of relationship is believed to be a common source of taxonomic difficulty in genera which have highly developed polyploid complexes.

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